CROSSOBOTHRIUM LACINIATUM AND DEVELOPMENTAL STIMULI IN THE CESTODA.

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In the spiral valve of the "sand shark" (*Carcharias littoralis*) taken from the Woods Holl region there is found in a large majority of the specimens examined the Cestode, *Crossobothrium laciniatum*. This genus and species was first described by Linton ("Rept. U. S. F. Com." for 1886), and in subsequent papers appearing in the same publication or in the "U. S. F. C. Bulletin," he has added further important notes, the whole making an accurate and satisfactory systematic description.

A striking feature of the species is the remarkable clearness with which the important features of Cestode structure can be demonstrated. The water vascular system, main trunks and flame-cells can be seen in the fresh specimen with the greatest ease. Almost every detail of the complicated reproductive organs is seen in well-stained whole mounts of the motile proglottids and much of this in specimens freshly prepared. The mode of using the suckers on the head, the activities of the motile proglottids and their mode of egg-laying and the development of these eggs in sea-water as far as the six-hooked embryo are all easily demonstrated. Moreover, there occurs in the cystic duct of the squeteague (*Cynoscion regalis*), a not uncommon food of the "sand shark," a tetrabothrian larva which, if not the larva of *Crassobothrium laciniatum*, probably belongs to some very closely related form. This larva, which was first described and figured by Linton ("Rept. U. S. F. Com.," 1886), is again an extremely favorable object for study.

If it is possible to obtain conclusive evidence that this tetrabothrian larva of the squeteague is indeed the larva of *C. laciniatum*, we shall have but one gap in the life history of this species, viz., the transfer to the squeteague of the six-hooked embryo which develops in the open ocean.

Such favorable material it seemed to me might present, upon careful examination, facts which would be suggestive along the line of some of the general problems involved in Cestode parasitism and development in addition to the possible opportunity for fixing the life history of this particular form. With this in mind I have been collecting all the data bearing upon the life history and during the summer of 1902 I made the first of a series of experiments in infection which I hope to continue and which may lead to more precise knowledge concerning the identity of the larva found in the squeteague.

I wish in this paper to describe the important features in the structure of the motile proglottids, its egg-laying and other activities, to give some observations on the larva from the squeteague and to discuss the view point which my study of the development in this and other Cestodes has suggested to me.

The Motile Proglottids.

When an incision is made in the spiral valve of an infected "sand shark" the Cestode is frequently found in such abundance that, as the elongated bodies and the motile proglottids writhe about in the chyle, one often wonders how there can be enough nourishment left for the host. I can confirm Linton's record, of "sand sharks" taken at different times, that in the great majority of individuals there are literally hundreds of this parasite in the spiral-valve to the exclusion of all others. When the parasites are examined in sea-water the alternate protrusion and retraction of the bothria, as described by Linton, can be observed for hours. When a scolex is compressed on a slide the flame cells of the water vascular system can be observed for a considerable time before they succumb to the abnormal conditions.

The ripe proglottids which can be pulled from the long strobilæ or found loose in the intestine are very active and constantly changing their shape. A typical outline in a partially extended condition is represented in Fig. 1, and the fully elongated condition is represented on a smaller scale in Fig. 2. At the anterior tip I have found in preserved specimens minute projections which have the appearance of cilia (*c*), but which will probably prove upon examination in the living specimen to be minute spikes similar to the larger ones on the penis (*p*).

The four ear-like flaps at the posterior end which give the strobila its characteristic appearance are frequently curled back and outward, giving the posterior end a quite different outline. In the living specimen I have frequently seen masses of sperm ejected from the penis, but my records of this do not mention

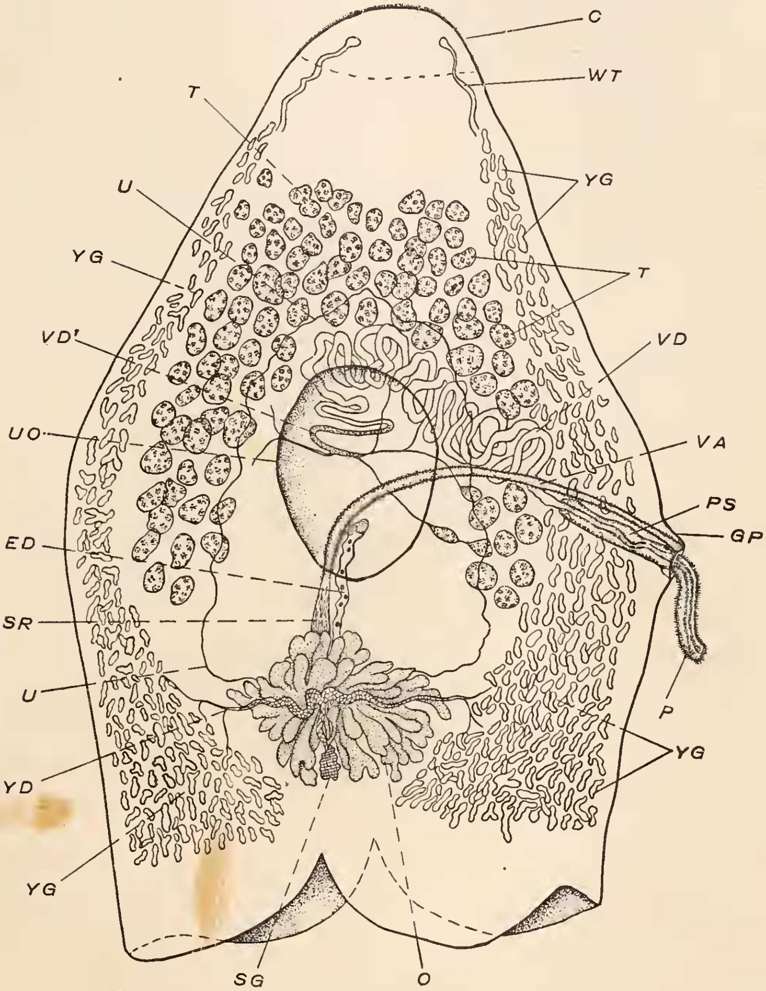

FIG. 1. Reproductive organs of a motile proglottid of *C. laciniatum*. *C*, cilia-like spikes at anterior tip; *ed*, egg duct from shell gland to uterus; *gp*, genital pore; *o*, ovary; *p*, penis; *ps*, penis sheath; *sg*, shell gland; *sr*, seminal receptacle; *t*, testes; *u*, uterus; *uo*, uterus opening through which the eggs escape; *vd*, vas deferens; *vd'*, denser inner end of same; *va*, vagina; *wt*, large water vascular tube; *yd*, yolk duct; *yg*, yolk glands.

the condition of the female organs in the proglottids thus observed. There are four main water vascular tubes. The larger pair lie on the same side of the body as the uterus opening and in the majority of cases one or both of them can be traced to a bulb-like enlargement on either side near the anterior tip of the proglottid. Posteriorly each one seems to end in the angle of the broadly wedge-shaped concavity formed by the projecting flaps. They here seem to end blindly against the cuticle which is perhaps perforated. There is no cross connection between these two vessels nor any common posterior opening such as is frequently stated to occur in *Tænias*. The second pair of main trunks are vessels of much smaller diameter and lie on the other side of the flat body immediately under the larger pair. Anteriorly they can sometimes be traced a little farther forward than the bulbs of the larger vessels, but do not seem to end in an enlargement. It is almost impossible to follow these smaller trunks for any distance posterior to the penis as the yolk glands are here closely packed together and obscure everything else.

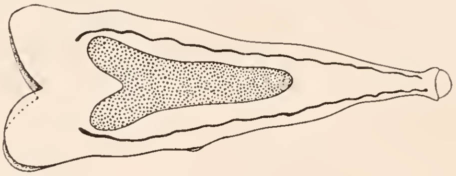

FIG. 2. Ripe motile proglottid fully extended, showing full uterus and the larger pair of water vascular trunks.

When the proglottids are examined alive much of their structure is obscured through the presence in the parenchyma of the highly refractive and closely packed granules of calcium carbonate. A very easy way of ridding the proglottid of this and preparing it for immediate examination is to use ten per cent. nitric acid and the pressure of a cover-glass. This dissolves the calcium carbonate and leaves the specimen quite transparent. This is a valuable method for the rapid examination of the principal organs, but for the finer details one of course needs more careful fixation and a good stain. I have found corrosive sublimate with about five per cent. acetic acid followed by Czokor's alum cochineal an excellent combination for the demonstration of the features given below.

The cirrus (*p*, Fig. 1) is eversible, working on the same principal as a Nemertean proboscis, a type common in Cestodes. From its base the much-coiled vas deferens (*vd*) leads away and is found throughout these coils crowded with sperm. At its inner end it has a denser wall and is of less diameter for a short distance (*vd*) and then divides into the vasa efferentia which can be seen radiating to the area in which the testes are located and in favorable cases followed down to the testicular follicles themselves (Fig. 1).

The vagina (*va*) which opens on the genital papilla just above the penis will be seen in the figure to pass inward and curve around backward, passing behind the mass of finger-like follicles which constitutes the ovary (*o*). It is here enlarged into the

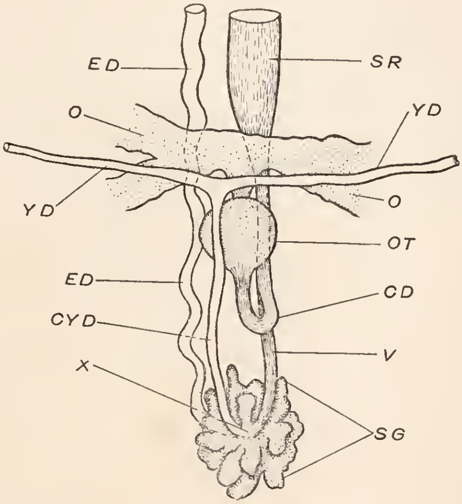

FIG. 3. Ducts of female complex with ovary lobes left out and ducts reflected slightly to show connections. *cd*, duct from oötype to inner end of vagina; *cyd*, common yolk duct; *ed*, egg duct; *o*, ovary; *ot*, oötype; *sg*, shell gland; *sr*, seminal receptacle of vagina; *v*, inner end of vagina; *x*, meeting place of ova and yolk; *yd*, right and left yolk ducts.

seminal receptacle which will be found full of sperms. Lying among the posterior lobes of the ovary is the shell gland (*sg*) to which the yolk is delivered from a common yolk duct formed by the union of a single yolk duct (*yd*) coming from either side. Extending anteriorly from the shell gland and beneath the ovary in this figure is the egg duct (*ed*) which conveys the eggs to the uterus. The complex of ducts in this region is shown in a reconstruction from sections represented in Fig. 3. The lobes of the ovary which are packed closely around the ducts are here omitted. This figure may be compared with what is shown in Fig. 1, where some of the same parts appear. The lobes of the ovary all converge upon a right and left portion (Fig. 3, *o*) and these main parts, on uniting, open posteriorly into a spherical cavity (*ot*) with thick walls, which is probably where the ova and sperm meet. A duct (*cd*) passes from this cavity to the inner end of the seminal receptacle (*sr*) and thence straight back to the shell gland (*sg*). Into the shell gland the common yolk duct (*cyd*) opens and from this common meeting place of the yolk and fer-

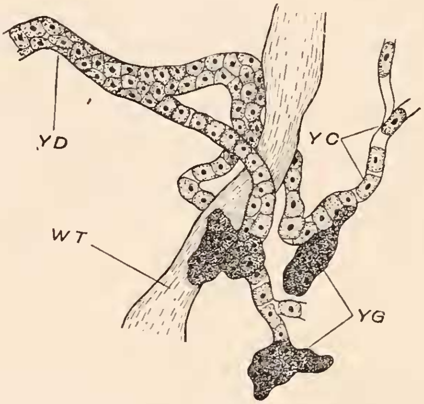

FIG. 4. Branching of yolk duct to yolk glands. *yd*, yolk duct; *yc*, yolk cells in duct; *yg*, yolk glands; *wt*, large water vascular tube.

tilized ova, after the acquisition of a shell, the fully formed egg passes up the egg duct (*ed*) into the uterus.

The right and left yolk ducts branch as they reach the areas of the yolk glands on either side and some of the branches may be seen going to individual yolk follicles (Fig. 4). These main branches are often found closely wrapped around the large water vascular tubes (*wt*) of either side. Yolk cells (*yc*) may often be found on their way down these ducts and accumulated in large numbers at their median ends. They are also seen in the short ducts which run from one yolk gland to another in all parts of the mass. The yolk-producing organ consists of follicles densely packed with yolk cells and distributed in the proglottid as the figure indicates (*yg*, Fig. 1).

Fig. 1 represents a specimen killed under pressure and in which the uterus had been ruptured and the eggs squeezed from the oval hole represented by the dark outline in the center of the proglottid. Very much the same sort of a hole is left when the proglottid ruptures itself at this point in the normal egg-laying. The extent of the uterus cavity is indicated by the outline (*u*) in the figure. The condition of the intact uterus and the place of its rupture will be explained in describing the egg-laying of the ripe proglottids.

Activities of the Motile Proglottids.

The proglottids of *Crossobothrium laciniatum* are an extreme case of what is usually termed the "motile" condition. So definite are their movements and activities that one is constantly thinking of them as though they were individual animals of a species entirely distinct from the parent scolex. When observed in the chyle they are seen writhing about, contracting and elongating rhythmically and bending their bodies into an arch along the axis of breadth, now one way, now another. If we measure the maturity of a proglottid by its size and the number of eggs accumulated in the uterus the conclusion is reached that the proglottids as taken from the spiral-valve are of diverse ages, for one finds a considerable variation in the number of eggs accumulated in the uterus and a correlated variation in the size of the proglottids.

When placed in clean sea-water the smaller proglottids do not lay their eggs, while the large ripe ones will almost immediately do so. These facts seem to indicate that the proglottids may be shed off from the strobila some time before they are ripe and remain in the shark's intestine until they are fully loaded with eggs and ready for the laying. The enormous number of proglottids usually found in a single spiral-valve is another fact in favor of this conclusion. On the other hand fully mature proglottids are frequently found on the end of a strobila (Fig. 5), showing that they may mature while still attached to the parent stock.

When carefully examined the ripe proglottids at the posterior end of a strobila (Fig. 5) or the mature motile proglottids found free in the chyle show a breast-like protuberance upon that face on which the uterus opens. The resemblance of this to a breast is heightened by the existence of a nipple-like prominence at the summit, as is shown in the side view given in Fig. 5. The general protuberance is caused by the distension of the uterus, though it sometimes seems to be enhanced by a concavity on the opposite face of the segment as the dotted line of the figure indicates. Motile proglottids when in this ripe condition show, if examined in the chyle, the ordinary writhings and indefinite locomotor movements noted above. If, however, a number of these ripe and full proglottids are transferred from the chyle into clean sea-

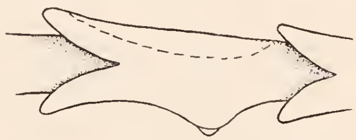

FIG. 5. Side view of a ripe proglottid.

water the egg-laying will presently be observed. In making observations on this process I was accustomed to select carefully ten or a dozen proglottids which seemed fully ripe and transfer them all together into a dish of clean sea-water. When this was done it was found that about eight out of ten thus selected laid their eggs in three or four minutes. Any of those remaining might lay after a little longer period or not at all. A similar reaction of whole chains of proglottids is recorded by Schauinsland (Jena, Zeitsch. 1886), for *Bothriocephalus latus*, *Trianophorus nodulosus* and *Ligula simplissima*.

When proglottids of *Crossobothrium* are taken at random and thus placed in sea-water only a small proportion, no more than one fourth or one fifth, will ever lay their eggs. When the small proglottids which have only a few eggs in the uterus are thus taken no egg-laying follows in any case.

That the proglottids as found in the spiral-valve at any one time are not all of same maturity is thus clearly shown and I think we are justified in the conclusion that these immature proglottids tend to remain in the spiral-valve until they become fully ripe and then to pass out with the fæces, even though their early detachment from its strobila may have been premature and caused by the outward passage of the excreta or the contraction of the intestine.

The manner in which the egg-laying proceeds in any single proglottid thus placed in sea-water is a very interesting thing to watch. Extreme writhing movements of a quite definite sort begin at once. The proglottid bends along its axis of breadth until it is almost a closed ring, the pointed anterior end sometimes passing into the angle made by the posterior flaps (Fig. 2) and thus reminding one of an acrobat who could bend backward until his head should be thrust between his legs from behind, then the proglottid straightens and the bend is reversed, it

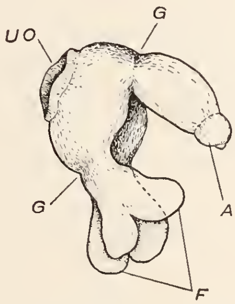

FIG. 6. Proglottid in the act of egg-laying seen from the side. Lettering same as for Fig. 7.

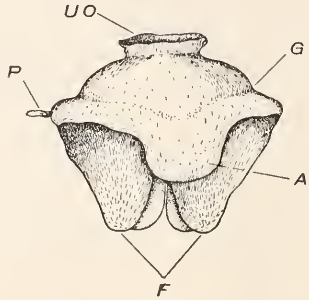

FIG. 7. Proglottid at close ot egg-laying seen from anterior end. *a*, anterior end ; *p*, penis ; *g*, groove marking outline of uterus ; *uo*, ruptured area through which the eggs escape.

straightens again and bends into the first position and so on; these motions continue until the nipple-like prominence of the protruding body bursts and the liberated eggs gush forth. When the break occurs the extreme violence of the writhing ceases and the proglottid bends backward rather more than forward (Figs. 6 and 7) until all the eggs have been expelled, when a gaping hole is presented (Figs. 6 and 7) where once was the distended uterus. Even when there is hardly an egg left within it, the straining movements of the proglottid continue as though it were making sure that not a single egg remained. Figs. 6 and 7 represent proglottids in which the egg-laying had been almost accomplished and show the characteristic attitude of the proglottid from a front and side view.

Proglottids which have thus stripped themselves of their eggs may continue to live in sea-water for a day or two, but I have not experimented with them to ascertain how long their existence may be prolonged.

The rupture of the uterus may be very readily produced in a proglottid having any considerable accumulation of eggs, if a little pressure is applied with a cover-glass or otherwise. But the process above outlined is something brought about spontaneously by the proglottid itself after it is transferred to sea-water. Proglottids which have been artificially compressed in killing, for whole preparations almost always have the uterus ruptured and the eggs discharged. They then present the appearance shown in Fig. 1, of a large oval hole opening into the uterus cavity, while the boundaries of the latter can be traced as a very delicate outline still conforming to the general outline of the full uterus. A proglottid which is in the last stages of egg-laying after the spontaneous rupture of its uterus shows the same sort of opening, but perhaps more widely distended. Such specimens which were killed without compression are shown in Figs. 6 and 7.

My observations are then that the proglottids when large and having the uterus full of eggs (Figs. 2 and 5) will, by a quite definite series of muscular contractions and writhings, rupture the nipple-like prominence at the summit of the protruding uterus (Fig. 5) and allow the eggs to gush forth, the proglottid continuing its writhing movements in a less pronounced degree even after all the eggs have been shed (Figs. 6 and 7). The fact that this egg-laying occurs immediately after the ripe proglottid is transferred from the chyle to clean sea-water will, I think, convince any one that the same process occurs when a ripe proglottid of *Crossobothrium* passes in the normal course of its existence out of the shark's cloaca into the water of the ocean. We may conclude I think that such a proglottid, upon coming into contact with the sea-water outside, goes through muscular contractions similar to those observed in the laboratory and lays its eggs free in the open ocean, and that these pelagic eggs are thus widely scattered. The short period between the first contact with the outer water and the egg-laying indicates that the infection of the intermediate host is, by means of countless embryos, developed in the open ocean and not by the eating of the intact proglottids with their contained eggs.

Egg Development.

On collecting the eggs laid by proglottids in the laboratory and placing them in dishes in which the sea-water can be kept reasonably pure, development ensues as far as the six-hooked embryo stage which I have represented in Fig. 8, drawn from the living specimen. I did not succeed in obtaining embryos beyond this stage, and therefore cannot say whether the embryo

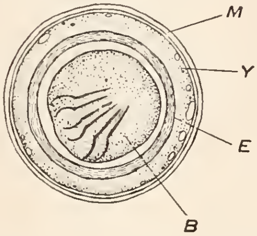

Fig. 8. Six-hooked embryo of *Crossobothrium laciniatum*. *m*, egg membrane; *y*, remains of outer envelop; *e*, ectoderm of Schaunisland; *b*, six-hooked embryo.

enters the next host in this condition or as a ciliated larva (Schauinsland, "Bothriocephalidæ," '86) which subsequently hatches from the embryo figured.

In the common Tænias and those Cestodes which have similar hosts and conditions of life-history, the fertilized eggs on passing into the uterus develop *there* into six-hooked embryos and remain in that stage until they reach the tissues of the intermediate host. In the Bothriocephalidæ, Schauinsland describes *B. rugosus* as having such an intra-uterine development as far as the six-hooked embryo, and *B. latus*, *Trianophorus nodulosus* and *Ligula simplissima* as producing eggs which develop only when they reach the water. In the last three species the eggs accumulate in the uterus in the condition of resting oösperms surrounded by their yolk and the egg-shell, but do not develop until they are laid in the water by the parent proglottid after this has left the host's intestines.

My material was prepared for the general anatomy rather than for this particular point, and the egg capsules are greatly shrunken, but as nearly as I can make out from a careful examination of the uterine eggs they are all in the condition above noted, viz., a resting fertilized ovum plus the yolk cells and egg capsule. In Cestodes having this mode of development, therefore, the eggs accumulate in the uterus, but do not develop until they are laid by the proglottid. The resting stage is comparable to the resting condition known in many forms which lay winter eggs or eggs which develop only after a considerable time. In any given proglottid such Cestode eggs are of diverse ages, depending upon how long they have been in the uterus, but are all alike inhibited from development until the proper conditions are present. Upon contact with the external water this resting stage is stimulated, or, we might say, some inhibition is removed, and development ensues, continuing as far as the six-hooked embryo. Whether there is some specific thing in the sea-water which can be fixed upon as the stimulus to development I have not ascertained, but it has seemed to me quite possible that the stimulus can be located in some specific chemical constituent of the sea-water.

From what we know of other Cestodes it is unlikely that the six-hooked embryo of *Crossobothrium* can develop further in the water, and that if this embryo does not find the appropriate stimulus for further development by meeting with its next host it must perish. What this next host is one would perhaps discover as much by accident as by the most persistent work. Could I clearly demonstrate that the larva found in the squeteague is the young of *Crossobothrium laciniatum* — and there is a good deal ot general evidence that this is the case — I think that the nature of the squeteague's food (young herring, adult herring, menhaden, etc. — Peck, "Sources of Marine Food," U. S. F. C. Bull., '95) would lead us to suspect that the six-hooked embryo, instead of passing directly to the squeteague, might have an intermediate host like the menhaden, herring, or some fish which feeds upon the microscopic elements in the sea-water.

Developmental Stimuli in the Cestoda.

To one examining closely the present trend of opinion regarding the process which our nomenclature still designates as fertilization it is, I think, quite apparent that the evidence and conclusions so logically and convincingly set forth by R. Hertwig[1] are gaining a wide acceptance both among special workers and among those who are viewing the data with a somewhat broader perspective. The details of Hertwig's paper had been already accepted by some of the investigators whom he cites, and so far as they concern the Protozoa they are mentioned by Calkins in his recent book as well-established facts, but this cannot detract from the able manner in which Hertwig has summarized these facts and indicated the important conclusions to be drawn from them. The work which to most persons offers convincing evidence of the twofold nature of the process we have been calling normal fertilization is the work in "artificial parthenogenesis" initiated by Loeb and Morgan. One could hardly ask for a more convincing proof that the union of the germ plasms and the "developmental stimulus," as Hertwig calls it, are distinct and separable phenomena although they have become almost indissolubly connected with one another throughout the Metazoa.

It having been shown in these experiments so far as they have now gone that a stimulus to development may be operative entirely independent of any union of the germ-plasms, as for example in the development of eggs of echinoderms or worms upon treatment with salt solutions and other stimuli, we should I think seek no less for the converse proposition, viz., *the union of the germ-plasm and the absence of developmental stimulus* (as evidenced by the absence of development) *while the oösperm continues its life.* We should then seek for the proper stimulus to this resting condition and by means of this stimulus initiate at will the developmental changes. To illustrate by a hypothetical case, suppose we could have a form where it were possible to bring about at will the union of the ovum and spermatozoön and their nuclei but by subtracting

[1] "Mit welchen Recht unterscheidet man geschlechtliche und ungeschlechtliche Fortpflanzung?" *Sitz. Ber. Gesel. f. Morph. und Physiologie in München*, Nov., 1899. Translated in *Science*, N. S., Vol. XII., no. 312, Dec. 21, 1900.

the "developmental stimulus" to have the resulting oösperm go into a resting state which would result eventually in its death unless the "stimulus to development" intervened to start a new cycle. If this developmental stimulus, or some substitute for it, and its action were accurately known we might apply it at will at any time after the union of the germ-plasms was completed, and so long as the oösperm remained alive it would respond by beginning the new cycle of development.

In the thorough understanding of the two apparently distinct processes involved in fertilization as hitherto understood we should I think be greatly aided by the investigation of the problem just outlined which is the *converse* of that brought out by the work on "artificial parthenogenesis."

We have, it seems to me, cases of normal development which are parallel to this converse proposition in just the same way that normal parthenogenesis is a parallel to the artificial development induced by salt solutions and other stimuli. These cases are seen in the development of those forms in which the fertilized egg has a long resting stage. Where freezing or desiccation is necessary for such subsequent development, this condition may be regarded as one of the developmental stimuli, although if one tries to picture how a state of affairs necessitating this particular condition could have arisen in the past he must, I think, feel certain that though extreme cold or dryness may now be a necessary factor it must originally have been unnecessary if not a thing fatal to the further existence of the organism.

Any one familiar with biological literature can readily recall numerous cases of eggs with longer or shorter resting periods following upon the union of the germ plasms. The particular case I call attention to is that presented by those Cestoda which in their development have *resting fertilized eggs* gradually accumulating in the uterus as in the case in *Bothriocephalus latus*, *Trianophorus nodulosus*, *Ligula simplissima*, etc., and in *Crossobothrium laciniatum*. On referring to the description which has been given of the production of the eggs and their extra-uterine development it will be seen that this illustrates particularly well what I have termed the converse of artificial parthenogenesis and that the hypothetical case which I set forth on page 137 might be substituted almost word for word for a description of what occurs in one of these Cestodes.

In addition to the phenomenon of a resting stage in their early development the Cestodes just mentioned, and indeed all other Cestoda, present in their subsequent life history a feature which I have found interesting when considered in connection with the primary "developmental stimulus" which starts the oösperm upon its course. Such a consideration of the subsequent facts of Cestode life history may perhaps widen our conceptions regarding the nature of one of the two phenomena which exist side by side in normal fertilization. How this is will be easily apparent if we recall the life history of *Crossobothrium* or any Cestode having a similar extra-uterine development.

The female reproductive organs of each proglottid produce ova which on being fertilized become surrounded by their yolk supply and encased in a tough shell. Without undergoing any developmental changes they accumulate in the uterus where they remain in this condition until the time of egg-laying. They are thus of very diverse ages if we date the age of each from the time of the entrance of the spermatozoön, but all are in the same *resting unicellular state.* We have here the union of the germ plasms, but the stimulus to development delayed for a period which is long or short, depending upon the age of the individual oösperm. The stimulus to development is normally found in the contact with the outside sea-water when the eggs are shed, for the cleavage begins only when they are thus set free. Development proceeds so far as the six-hooked embryo stage when death ensues unless the proper host is found. In the case of *Crossobothrium* there is perhaps a primary intermediate host between the six-hooked embryo and the squeteague in which case the six-hooked embryo which infects this intermediate host receives a stimulus to development which sends it so far as the resting stage which is attained in that particular host, and here it stops and eventually comes to naught unless it is carried into the next host, the squeteague, where it finds a new stimulus to further developmental changes and attains in the cystic duct of this fish its development to the full structure of a tetrabothrian larva.

Here again death ensues unless the next stimulus in the series is forthcoming, viz., the contact with the digestive juices of the "sand shark's" stomach. When this stimulus is furnished the tetrabothrian surviving the wreck of its teleost host develops into the final adult condition.

The foregoing is stated in sufficiently general terms to be applicable, *mutatis mutandis*, to any Cestode having an extra-uterine development and whether or not the life history outlined for *Crossobothrium* is the correct one does not affect the general conception of Cestode life history which I am attempting to portray.

In stating the above I have spoken of the reaction of the embryo of a given stage to its particular stimulus just as I spoke of the reaction of the oösperm to the stimulus which initiates the whole cycle. If we ask ourselves what is the essential nature of the reaction of the oösperm to the delayed developmental stimulus we must designate it as primarily a reaction manifest in so many cell divisions and subsequent differentiations. In what does the result produced by any one of the stimuli, which, if the embryo runs its whole course, become applied to each of the successive stages, differ from the result produced by the stimulus which acts upon the oösperm? Cannot the result in each instance be formulated in the same way, viz., that the stimulus causes cell divisions and subsequent differentiation? And should we not speak of all of them as "developmental stimuli"?

The exact nature of the stimulus at each stage is a thing which in spite of many technical difficulties would be open to investigation and something which we may hope eventually to understand, but however diverse the stimuli might be we should still have, as above stated, changes of the same nature resulting from each successive stimulus. The stimulus which is in the first instance something in connection with the sea-water is probably in the other cases a change in nourishment incident to the change of hosts, but in every case the *result* of the stimulus may be stated in the same general terms, viz., cell division and subsequent differentiation which ends in a condition of stable equilibrium in which the animal finally perishes unless the next stimulus is forthcoming.

Viewing then the life history of such a Cestode from this point of view we have first the union of the germ plasms followed by a resting stage of varying duration. A stimulus furnished by the contact with the sea-water when the eggs are laid brings about the changes resulting in the six-hooked embryo. This embryo when it receives a certain stimulus (condition of nourishment or otherwise) from the intermediate host goes as far along the course of development as the mid-larval stage and stops again. On reaching the stomach of the final host the last stimulus of the series is furnished and the adult condition attained.

In those Cestoda which have an intra-uterine development, *i. e.*, forms in which a six-hooked embryo develops in the uterus, we find the primary developmental stimulus intimately associated with the fusion of the germ plasms as in the fertilization of most Metazoa, though in *Bothriocephalus rugosus* (Schauinsland, '86) the intra-uterine development may not begin for several weeks after the eggs have begun to pass into the uterus cavity. In such cases the comparison between the primary "developmental stimulus" and the developmental stimuli which follow is of course not so patent, although it is none the less legitimate. Whether what I have called a "*developmental stimulus*" in these several cases shall be found eventually to be some new condition which the egg or embryo meets or be found to be the removal of some existing condition which has been inhibiting the development is of no consequence here since the removal of an inhibition may be spoken of as a stimulus, and since the important thing is not the nature of the stimulus but the similar reaction of the animal in each case.

In conclusion I may say that no facts not already familiar to students of Cestode life history have been set forth in the section of this paper just concluded, nor can it be claimed that the apparently two-fold nature of fertilization has not been in recent years more than once promulgated. The comparison between the reaction of the oösperm to the primary developmental stimulus and the reaction of the larval stages each to its special stimulus has interested me and it has seemed to me worth while to attempt the formulation of Cestode life history from this point of view. I also believe that the two-fold nature of fertilization has not yet reached such a point of general acceptance or rejection, but that it will bear further illustration in any case in which there are facts particularly germane to the question and with these two points in view I have attempted the foregoing formulation.

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